

A test of the provisioning hypothesis of recruitment control in Georges Bank haddock

Kevin D. Friedland

Abstract: The haddock (*Melanogrammus aeglefinus*) stock of the Georges Bank region of the US Northeast Continental Shelf displays a pattern of large, episodic recruitments. Among the hypothesized controlling mechanisms is the idea that recruitment events are related to provisioning of prespawning haddock by the fall bloom the year before. With the occurrence of a recent large recruitment event in 2013, it would be prudent to retest this hypothesis. Fall bloom magnitude was positively correlated ($r = 0.645$, $p = 0.005$) with haddock survivor ratio (recruits per spawning biomass), including data from the 2013 recruitment. This relationship identifies a pathway of bottom-up control of a resource species, thus focusing concern over recent changes in lower trophic-level productivity.

Résumé : Le stock d'aiglefin (*Melanogrammus aeglefinus*) de la région du banc de Georges de la plateforme continentale du nord-est des États-Unis est caractérisé par d'importants recrutements épisodiques. Parmi les mécanismes proposés pour expliquer ce phénomène figure l'hypothèse selon laquelle les épisodes de recrutement sont reliés à l'approvisionnement d'aiglefins pré-généseux par la prolifération automnale de plancton de l'année précédente. Il serait prudent, à la lumière de l'important épisode de recrutement de 2013, de valider à nouveau cette hypothèse. La magnitude de la prolifération automnale est positivement corrélée ($r = 0,645$, $p = 0,005$) au rapport des survivants (recrues en fonction de la biomasse de géniteurs) des aiglefins qui inclut les données du recrutement de 2013. Cette relation permet de cerner une voie de contrôle ascendant d'une espèce ressource, mettant ainsi en relief les préoccupations concernant les variations récentes de productivité dans des niveaux trophiques inférieurs. [Traduit par la Rédaction]

Introduction

It has been hypothesized that the recruitment of haddock (*Melanogrammus aeglefinus*) on Georges Bank (GB) may be influenced by the provisioning effects of the fall bloom on prespawning adults (Friedland et al. 2015). Since haddock tend to feed on detritivores like ophiuroids and amphipods, the mass flux of fixed carbon associated with a phytoplankton bloom may affect the energy flow to haddock on relative short time scales. The fall bloom would provide energy that haddock could invest into reproduction affecting fecundity and egg condition in females and (or) gamete production in males. Haddock females are also known to skip spawning in years with limited energy resources, which adds a further dimension to how provisioning may affect recruitment (Skjæraasen et al. 2020).

This hypothesis has stimulated considerable debate and productive discussion (Friedland et al. 2009). The original analysis supporting this hypothesis was based on a sample size of $n = 7$ and ran contrary to more classic hypotheses of recruitment control related to first feeding and larval retention (Platt et al. 2003; Buckley and Durbin 2006; Boucher et al. 2013). As is the case in fisheries and related fields, correlation may not always detect robust mechanistic linkages (Havens 1999), so there is a responsibility to monitor and test correlative relationships as new data become available. This is particularly important when there has been a change in the conditions or events that may affect the correlation. This may be the case with the GB haddock stock, which experienced the highest recruitment on record in 2013, a year

class not included in previous analyses (Finley et al. 2019). The purpose of this rapid communication is to test the patency of the relationship between GB haddock recruitment and the dimensions of phytoplankton blooms forming on GB in the fall prior to spawning. It is important to know whether the exceptional recruitment in 2013 can be attributed to the provisioning hypothesis and, more generally, whether the relationship holds with more than a doubling of recruitment data to consider beyond the original analysis.

Methods

The approach taken in this report is the similar to the original and subsequent analyses of the effects of fall bloom dynamics on haddock recruitment reviewed by Friedland et al. (2015). Only at those points where the analysis differs from previous methods will detail be provided. To provide context, the subject haddock stock is resident in the GB ecoregion (~51 000 km²; 39.95°N–42.17°N, 65.66°W–70.51°W) of the US Northeast Continental shelf. The analysis is based on the relationship between the magnitude of the fall bloom and the survivor ratio or the recruits per spawning stock biomass (SSB) ratio of the haddock population. In earlier analyses, the ratio was based on assessment data; here, it is based on time series-corrected survey indices from the Northeast Fisheries Science Center bottom trawl survey using the GB haddock strata set. SSB in year i was calculated from the spring survey catches as biomass (kg) per tow of

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K.D. Friedland.* National Marine Fisheries Service, 28 Tarzwell Dr., Narragansett, RI 02882, USA.

Email for correspondence: kevin.friedland@noaa.gov.

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Table 1. Survey indices of spawning stock biomass (SSB, kg·tow⁻¹), age-1 recruitment (R1, number·tow⁻¹), survivor or recruit per spawner ratio (R1/SSB), and logarithmic transform of the ratio.

Recruitment year	SSB	R1	R1/SSB	log(R1/SSB)	Base		Range		<i>n</i>
					Magnitude	Duration	Magnitude	Duration	
1999	6.53	1.85	0.28	-0.55	—	—	7.57	4.00	3
2000	15.04	10.01	0.67	-0.18	14.13	8	13.96	7.89	27
2001	4.89	0.16	0.03	-1.49	—	—	11.43	6.00	12
2002	18.50	0.08	0.01	-2.34	8.38	4	8.92	4.33	27
2003	15.61	112.01	7.17	0.86	10.23	5	12.98	6.70	27
2004	33.20	0.81	0.02	-1.61	—	—	7.26	5.00	6
2005	11.37	1.99	0.18	-0.76	10.41	7	10.06	6.75	24
2006	14.66	0.87	0.06	-1.23	—	—	7.16	5.00	9
2007	31.01	1.84	0.06	-1.23	11.71	6	12.67	6.56	18
2008	23.26	1.49	0.06	-1.19	—	—	9.13	5.00	9
2009	19.54	0.41	0.02	-1.68	—	—	6.16	4.00	6
2010	31.47	57.89	1.84	0.27	—	—	—	—	—
2011	9.45	18.70	1.98	0.30	10.74	5	10.35	4.78	27
2012	11.97	3.15	0.26	-0.58	11.25	5	11.25	5.00	18
2013	19.81	602.33	30.41	1.48	15.23	7	15.18	7.00	27
2014	44.29	17.47	0.39	-0.40	7.96	5	7.50	4.68	19
2015	41.98	15.76	0.38	-0.43	22.96	13	17.52	9.63	24
2016	40.44	19.07	0.47	-0.33	11.40	7	11.38	7.00	25
2017	50.52	1.72	0.03	-1.47	8.55	6	8.70	6.13	24
2018	34.66	0.80	0.02	-1.64	—	—	—	—	—

Note: Data include bloom magnitude (mg·m⁻³·8-day period) and duration (number of 8-day periods) for the base conditions of STARS parameter (Base) and mean of the ensemble of estimates using ranges of parameters (Range), with the number of detections using the range parameters (*n*).

mature fish each year, weighted by maturity and weight at length.

$$SSB_{\text{year } i} = \sum M_{\text{len}} \times N_{\text{len}} \times W_{\text{len}}$$

where M_{len} is the maturity at length, N_{len} is the stratified mean number at length, and W_{len} is the weight at length. Recruits were represented by the stratified mean number per tow of age-1 haddock in year $i + 1$. The logarithm of the survival ratio was used in the correlation analysis.

Bloom magnitude (the sum of chlorophyll concentration during the bloom period) was calculated the same way as in previous assessments based on bloom periods identified with the change point algorithm STARS (Rodionov 2006). The STARS algorithm was parameterized with an α level of 0.1, a length criterion of 5, and a Huber weight of 3 as the base conditions. The approach was extended with the use of parameter ranges to increased bloom detection rates. In addition to the base STARS parameters, α was varied over the range of 0.05, 0.1, 0.15; length criteria varied over the range of 4, 5, 6; and Huber weight varied over the range of 2, 3, 4. Note that in previous assessments, blooms that exceeded a duration of nine 8-day periods were considered ecologically different from discrete blooms and were excluded from the analysis (Friedland et al. 2015). The chlorophyll data used in previous assessments were limited to data from only two sensors (MODIS and SeaWiFS) and were combined with an ad hoc method of time and area conversion factors. The chlorophyll concentration data are now derived from a merged multisensor ocean colour data product from Hermes GlobColour website (<https://hermes.acri.fr>) using the Garver–Siegel–Maritorena Model (GSM) algorithm to combine the data (Maritorena et al. 2010). The relationship between survivor ratio in year i and fall bloom magnitude in year $i - 1$ was tested with Pearson product-moment correlation. The time series were screened for the presence of serial correlation with autocorrelation functions, which would indicate the need to apply correlation tests corrected for autocorrelation (Pyper and Peterman 1998).

Results

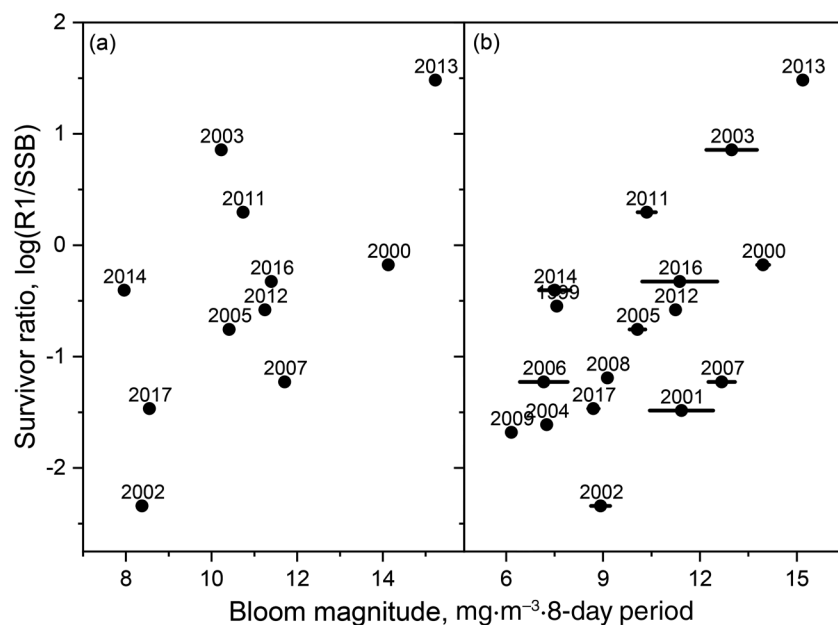
Using the base parameters in the bloom detection algorithm, 12 fall blooms were detected to potentially inform the time series of 20 recruitments over the period 1999–2018 (Table 1). Bloom magnitudes varied over the range of ~8–23 mg·m⁻³·8-day period. As noted above, blooms of duration greater than nine 8-day periods were excluded previously, and that was applied to the bloom detection in 2014 (relevant to recruitment year 2015 in Table 1). The correlation between the survivor ratio and bloom magnitude was 0.611 ($p = 0.046$) and is shown in the scattergram in Fig. 1a, which highlights the highest bloom magnitude and its associated recruitment in 2013. Neither time series had significant serial correlation; thus, a correlation test corrected for autocorrelation was not indicated.

Using ranges of bloom detection parameters, I detected 18 fall blooms to potentially inform the time series of recruitments. Mean bloom magnitudes varied over the range of ~6–18 mg·m⁻³·8-day period, which was based on multiple detections each year. The number of detections each year ranged from 3 to 27. As noted above, blooms of duration greater than nine 8-day periods were excluded previously, so again this selection criterion was applied to the mean detection in 2014. The Pearson product-moment correlation between the survivor ratio and bloom magnitude was 0.645 ($p = 0.005$) and is shown in the scattergram in Fig. 1b, which highlights the highest bloom magnitude and its associated recruitment in 2013. Neither time series had significant serial correlation; thus, a correlation test corrected for autocorrelation was not indicated.

Discussion

This updated analysis provides additional evidence supporting the hypothesis that fall bloom provisioning of prespawning haddock acts as a controlling factor over GB haddock recruitment. In addition to providing a correlative test with more observations, the current test includes an extreme recruitment that aligns with the highest bloom magnitude in the time series. As encouraging as these result would seem, it is important to remember that they do not address the relative role of multiple factors in

Fig. 1. Scatter between survivor ratio and bloom magnitude for estimates using the base set of STARS parameters (a) and with mean of the ensemble of estimates using the ranges of parameters (b). The error bars in panel (b) are 95% confidence intervals around the mean bloom magnitude.



shaping haddock recruitment (Friedland et al. 2015). The accumulation of further contrast in the recruitment data for haddock would suggest it might be possible to weigh the role of additional covariates in the recruitment process; that sort of research should be supported.

Recruitment control of haddock poses a number of ecological and management challenges. These recruitment events in haddock are so large that they not only affect the fishery for haddock, but also create food web imbalances affecting other species (Richardson et al. 2011). We are beginning to develop a refined view of bottom-up effects in marine ecosystems and their impact on upper trophic-level fishery yields (Capuzzo et al. 2018), which would not be of concern if primary production was in homeostasis. However, GB and the Northeast Shelf ecosystem is experiencing change in the physical environment and a concomitant decline in primary producers, dimming the prospects for continued yields of fishery species (Friedland et al. 2020). With building evidence of the linkage between fall phytoplankton blooms and haddock recruitments on GB, change in lower trophic-level production may have a focused effect on haddock in this region. We are faced with the reality that the failure to account for the effects of lower trophic-level change and variability may lead to unmet expectations and flawed fisheries management decisions and policy (Bentley et al. 2020). This is particular challenging in taxa with a long prerecruitment survival window such as haddock (Haltuch et al. 2019); however, the fishery management decisions for this stock would be improved by considering these and other ecosystem effects.

The recruitment process in marine fish such as haddock is complex and often dependent on multiple factors. For many species, recruitment can be mediated by maternal effects and the dynamic balance between growth and condition of parents and offspring subject to the feeding opportunities at the larval and adults stages (Brosset et al. 2020). However, maternal effects as a recruitment shaping control for haddock does not appear to be universal. In the Barents Sea, haddock appear to be impacted most by predation pressure on juvenile fish that can be traced to feeding interactions with Atlantic cod, *Gadus morhua* (Filin and Russkikh 2019).

The predation effect appears to respond to climate drivers related to thermal conditions that favor cod and thus produce a negative feedback on haddock juveniles (Durant et al. 2020). Like other broadcast spawners, the dispersal and retention of haddock larvae has been intensely studied and shown to be a necessary requirement for successful recruitment, but has yet to be shown to provide an explanation for haddock recruitment events (Boucher et al. 2013). Recent work suggesting that haddock larvae have a magnetic orientation sense that enhances their retention in nursery areas would be consistent with the assumed role of transport in recruitment (Cresci et al. 2019).

For many marine species, recruitment response to broadscale drivers is often coherent (Zimmermann et al. 2019), which suggests similar factors are at work on individual populations. This begs the questions of why haddock on GB appear to have such a distinctive pattern of recruitment in response to the development of fall blooms. One important factor to consider is the paucity of marine ecosystems with a prominent fall bloom. In the North Atlantic, there is a narrow band of latitudes with the requisite conditions to have a two-bloom system (i.e., spring and fall blooms; Friedland et al. 2016). The energy pulsed into the benthos of GB is mediated by the spring bloom but, more importantly, also by a highly variable fall bloom.

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